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THE SIGNIFICANCE OF THE COURTSHIP AND SECONDARY SEXUAL CHARACTERS OF ARANEADS¹

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BUT few observers have made special studies in those phenomena in spiders of which it is proposed to treat in the present communication. The first studies, by Canestrini, were inaccessible to me. The main work on the subject is that of Professor and Mrs. Peckham (1889, 1890). They have described in great detail the courtship of a considerable number of *Attidæ*, and have given excellent illustrations of the attitudes of the males. Then after an analysis of the phenomena in question they have criticized the views of Wallace (1889), and have accepted that part of the sexual selection theory of Darwin which accounts for secondary sexual differences on the basis of an esthetic discrimination by the female. The results of these studies have been generally accepted as one of the strongest confirmations of Darwin's views. In the introduction to their last memoir (1909) they have reiterated their arguments, with the addition of certain new and important observations. The next special work on this subject is my paper of 1903, in which is described in detail the courtship of certain *lycosids*, *agelenids*, *dictynids*, *theridiids*, *pholcids*, *epeirids* and *thomisids*. My general theoretical conclusions were quite different from those of the Peckhams: the adult male is excited simultaneously by fear of and desire for the female, and his courtship motions "are for the most part exaggerations of ordinary motions of fear and timidity. By such motions he advertises himself to the female as a male, but

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there is no proof that he consciously seeks to arouse her eagerness by esthetic display . . . there seems to be no good reason to hold that the female is actuated in her choice by sensations of beauty." Thus my opinion was opposed to Darwin's theory. The remainder of the literature on the secondary sexual phenomena of araneads contains for the most part only casual observations, without attempts at analysis.

I. SOME GENERAL MATING RELATIONS

For a correct understanding of the points at issue it would be very desirable to have ample data on the numerical proportions of the sexes, but unfortunately little is known on this head. What is known is brought together in another paper of mine (1908a); and there also it was found in the case of *Lathrodectus mactans* that the "average male ratio (number of the males divided by the number of the females) is 8.19, determined from a count of 41,749 newly hatched spiderlings." In this species the adults differ most markedly, and the young emerging from a cocoon are readily separable into two groups, distinguishable not only by size relations, but also, as specially indicated by me, by differences in the form proportions of the abdomina. Those spiderlings with a flatter dorsum and more anterior pedicel were considered to be males, for this is one of the characters in which the adults differ. However, none of these spiderlings were raised to maturity, though the attempt was made to do so; no differences in the internal genital organs can be found at the time of hatching, and occasionally (though rarely) nearly intermediate forms occur between the two groups of spiderlings. There is then room for doubt whether the two groups represent males and females, respectively, and the sex-ratio is not securely established from my results; it is rather in the nature of a strong probability. Beyond this case nothing definite is known about the numerical proportions of the sexes.

It is the general rule that the males mature earlier than the females, and the former do not live longer than a year. Promiscuous mating is general, a male impregnating a number of females, and a female receiving a number of males. I have seen a female of *Geotrecha pinnata* mating with two males in close alternation, two males of the theridiid *Ceratinopsis interpretes* embracing a female simultaneously, and I have described (1903) for *Theridium tepidariorum* as many as twenty-seven impregnations of one female. In the attid *Phidippus purpuratus* one male was seen by me to fertilize several females. Monogamy is exceptional, and would appear to occur in cases where the male seizes immature females by force, and where the male lives in a mating nest with a female. Many attids make such nests; in the case of *Phidippus purpuratus* I have frequently found pairs in such nests in the wild state but never found them to make such nests in captivity, where there is on the contrary promiscuous mating. McCook (1890) has brought together some of the literature on mating nests. In certain cases an adult male seeks out and sequesters an immature female, mating with her when she matures. The Peckhams (1889) found the only attid under their observation, "in which we saw males take possession of young females and keep guard over them until they became mature," to be *Philæus militaris*. A pair of *Drassus neglectus* was caught by me in a mating nest on June 16, last, and placed in a cage, where he built another nest around her; on June 23 he mated with her when she had just finished moulting and was still quite soft; in another case a male and an immature female were found in the same nest. A mature male of another drassid, *Prosthesima atra*, was repeatedly observed by me to hold an immature female, and on another occasion to grasp two such at once. In *Theridium tepidariorum* adult males wait upon the snares of immature females, and this has been seen by McCook (1890) and me in various epeirids. In *Lycosa ocreata* I found that

males pay no attention to immature females, while they do in *L. scutulata*. During the past summer I have seen males courting immature females in the attid *Zygoballus beltini*, the thomisid *Xysticus nervosus*, and the drassid *Chiracanthium inclusum*.

In some species, as notably epeirids and lycosids, pregnant females are hostile to males. But I have seen such females of *Theridium tepidariorum* and *Phidippus purpuratus* receive males, and on one occasion a female of *Geotrechapinnata* was interrupted several times during her cocooning by embraces of a male. Males appear to court any mature female, whether she be virgin or not.

II. SENSES EMPLOYED IN SEXUAL RECOGNITION AND STIMULATION

Here we have to consider briefly the rôles of hearing, touch, sight and smell.

There is no good evidence that spiders possess hearing, while the arguments of Wagner (1888) and especially the direct observations of Pritchett (1905, done under my direction) speak almost conclusively against such possession. Some spiders have stridulating organs, and in certain species these are limited to the male (*Theridium*, according to Westring), but no experiments have been made to determine whether the spiders react to the sounds produced thereby. I have recently found in the drassid genus *Geotrechapinnata*, where both sexes possess a stridulating apparatus, the spiders do not in any way indicate any perception of sound but perceive each other solely by touch. It is then fairly firmly established that the sexes do not recognize each other by hearing.

Touch is the dominant sense, and would appear to be the especial function of the jointed spines. In nocturnal species as well as in all snare-weavers it appears to be the only sense of sex-recognition.

Smell is possessed by spiders, but what organs sub-

serve it is not determined, beyond that it seems to be distributed over a considerable area of the body. The most careful study of it has been made by Pritchett (1905), while Petrunkevitch (1907) found it to be less keen than touch. It might be this sense that guides wandering males in their search for females. But I am inclined to believe it does not, for of pairs I have watched attentively in cages the male always appeared to find the female by either touch or sight, while if he is near her, but without seeing or touching her, he seems unconscious of her proximity. Further, when in the wild state a male approaches a female upon her snare, there seems to be no evidence that he constantly approaches her in the direction of the wind. Thus it is very doubtful whether scent has any part in sex-recognition in spiders, while it is the most usual mode of sex-recognition in insects.

Sight undoubtedly plays a considerable part in sex-recognition in certain diurnal species, determined for the attids by the Peckhams, and for the lycosids by me. These spiders, however, perceive readily only moving objects. But, as we shall see, it is not used for this purpose in the other spider families, not even in the diurnal thomisids. Thus I can not agree with Petrunkevitch's conclusion (1907) that "the sense of sight is beyond any doubt the only sense that guides hunting spiders on their hunting excursions and in finding the females during the mating period," for I have frequently noticed males of even diurnal attids and lycosids first recognizing the female by touch. And in the case of *Pardosa nigripalpis*, a species that always courts by light, it was remarked by me (1903): "In a double cage with a transparent glass partition, a male in one compartment and a female in the other, I have not seen a male court a female, though he certainly sees her through the partition; probably, then, it is touch of a female that impels him to courting activity." Numerous pairs were kept by me in such cages to test this point.

The senses of sex-recognition are, accordingly, touch in the first place and sight in the second, the latter important in only a few families.

III. DETAILS OF THE COURTSHIP PHENOMENA

It will be convenient for our present purposes, for it is based upon habitudinal differences, to divide the species on which observations have been made into the two categories of "snarers" and "hunters." The literature on the subject has been gleaned as thoroughly as possible; and my new observations of the past summer have been presented more fully than the others simply because they are here given for the first time.

1. *Snarers*

In *Dictyna volupis* Keys. mature males and females live together upon the web, which they appear to fabricate in common; the male is somewhat larger. In two cases the approach of the sexes was seen by me (1903): in one the male approached and seized the female; in the other case a male came face to face with a female, "then, each of them tapping upon the web with the first two pairs of legs, they moved backward and forward slowly. This lasted only two minutes, when they both became quiet half an inch apart; it was repeated again for a short period." These are the only observations on any cribellate form, and they do not indicate clearly whether rape or courtship by the male is the usual process.

For the Agelenids Menge (1843) described the approach of the male in *Agelena labyrinthica* as follows: The male climbs into the web of the female, taps on it with his palpi, but must sometimes wait for an hour before the female allows him to approach. "When she is complacent she places her legs close to her side, and the male embraces her with his legs and carries her into the funnel." In *A. navia* Walck., I saw the approach

of the male in two cases; in both there was nothing "to indicate a courtship; there was simply a cautious approach of the male," he touched her with his first legs, "and after he had found no sign of hostility on the part of the female he quickly seized her, and she was absolutely submissive in his grasp." In *Tegenaria durhami* Scop., in several cases, the male was seen by me to slowly approach the female upon her web, he tapping the latter with his fore legs as he advanced, the female occasionally also tapping in response, after which he would make a sudden rush at her. In these agelenids there are no courtship motions beyond tapping on the web, to which the female may respond, in like manner; the male seems to find her by touch, and after a cautious approach to seize her forcibly.

In *Pholcus phalangioides* Fuessl. I found (1903) no courtship; the male approaches the female very cautiously upon her web, and touches her gently with his legs; he always approaches her from beneath, and immediately drops from the web if she move at his touch. He finds her position by carefully pulling the lines of the snare.

In the theridiids a number of observations have been described. Menge (1843) found in *Linyphia triangularis* that the approaching male shakes the snare rapidly, to which the female responds by a similar motion. In *Theridium tepidariorum* C. Koch I have seen (1903) the approach of the sexes many times; when a male is placed upon a web of the female, she immediately signals to him by repeated jerks upon the lines of the web, sometimes moving towards him. This signalling is a sign of eagerness on her part, and "she makes it at no other time than when she is eager and notices the approach of a male of her own species. . . . The whole attitude of the male is that of combined timidity and great eagerness. . . . He tests the eagerness of the female, and finds her position upon the web, by grasping with the claws of his first pair of feet the web lines that she is

shaking by her signalling, and by drawing these web lines taut he feels her movements all the more distinctly; he approaches gradually nearer her, guided by her signalling, and finally makes a short rush toward her." The female often seems insatiable, even leaving food at times to approach the male, and the courtship is largely on her part, by signalling.

Similar signalling by the female was noticed by me in *Teutana triangulosa* Wolck. During the past summer I watched the process in *Theridium frondeum* Htz., where the female signals, and the male responds in the same way; the female had her rear turned towards him so that she could not possibly see him; in one case a female signalled to another female. In the case of the tiny *Ceratinopsis interpretes* Emert. I placed two males and a female together in a vial, where they spun a maze of lines in a short time, but I observed quite a different approach of the males. The female does not appear to signal, but the male makes a quick rush at her, and taps her rapidly with his legs until she becomes submissive with contracted legs. A male acts towards her as he would to another male, seemingly aggressive, until she becomes immobile; they find one another by touch communicated along the web lines, not by sight.

In the Epeirids a number of genera have been studied. In *Pachygnatha listeri* Menge (1866) saw the male seize with his chelicera those of the female. In *Argiope* (Peckham 1889, McCook 1890, Emerton 1883) the male courts the female by pulling the radii of her snare, and she responds in the same way. "If matters be favorable, the male draws nearer, usually by short approaches, renewing the signals at the bolting places. Sometimes this preliminary stay is brief; sometimes it is greatly prolonged" (McCook). In the case of *Acrosoma gracile* Walck. I dropped (1903) a male upon the web of a female, and as soon as he touched her (within five minutes) he copulated; no special courtship was seen. In the genus *Epeira* the approaches of the male are well known from

the observations of Walckenaer (1837), Menge (1843, 1866), Termeyer (1866), Lendl (1886), McCook (1890) and myself (1903, 1908*b*). The male approaches the female cautiously upon her web, locating her and testing her eagerness by pulls upon a radius, she responding gently to his signals when she is eager, otherwise she makes a sudden rush at him in which case he swings free from her web on a particular line of his own.

When we sum up what is known of snare-weavers, it appears that in them sex-recognition is always by touch, by tapping or pulling of the web. In a few cases (*Tegenaria*, *Ceratinopsis* and perhaps *Dictyna*) the male attempts to capture the female by storm; but more generally he approaches very cautiously and timidly, signalling to the female. When there is a courtship it is one of line signals, and sometimes (*Theridium*) the female seems the more eager and active in the courtship.

2. Hunters

For the drassids, most of which are nest makers and essentially nocturnal, there are the following observations. Menge (1872) placed together a male and female of *Melanophora nocturna*, whereupon the male immediately embraced the female without courtship; and he observed (1873) a similar forcible rape in *Chiracanthium oncognathum*. In *Clubiana trivialis* he found (1873) that the male makes a small saccular nest next that of the female, and that he knocks, sometimes for days, upon her nest wall before she allows him to enter. During the past summer the following observations were made by me. In *Drassus neglectus* (Keys.) an adult male appropriates an immature female, seals her in a mating nest, and mates with her just after her last moult; in one case the male found the female in the cage by touch alone (I could see no evidence of recognition by sight), and rendered her passive by gentle tapping with his first legs. The male of *Chiracanthium inclusum* Htz. also finds the female by touch, and tries to subjugate her

by gentle tapping with his exceedingly long first leg pair. In *Prosthesima atra* (Htz.) the male appropriates immature females; there is no courtship, beyond a tapping with the legs. The two sexes of *Geotrecha crocata* (Keys.) do not recognize each other by sight; a mating was observed, but no courtship preceded it. Also individuals of *Geotrecha pinnata* Emert, do not recognize one another by sight, perceiving each other only when nearly in contact—so probably by air pressure (touch); they run rapidly, and in the open on overcast afternoons, so they might be expected to form visual images, but they showed no signs of recognizing each other by sight. After a mating the male always leaves the female for a few moments, then returns to her again, and at such times he moves in an irregular path, feeling for her. He recognizes her by contact, and taps her legs with his own until she becomes quiet. In one case a female accepted in succession and repeatedly the embraces of two different males, one of which had only a single palpus; here the female exhibited no choice whatsoever. In the drassids, accordingly, sex recognition is wholly by touch; the male sometimes seizes the female by storm, sometimes subjugates her by tapping with his legs.

In the thomisids we have to do with diurnal spiders that lie in wait for their prey, without constructing web lines (except drop lines); they are mostly found upon vegetation above the ground. The male is more nimble than the female and smaller, sometimes much smaller. In *Micrommata virescens* Menge (1874) saw the male jump upon the back of the female. In *Xysticus stomachosus* Keys. I found (1903) that the sexes recognize each other by sight to some extent, but that the male pays no particular attention to the female until he touches her, when he quickly seizes one of her fore feet with one of his and nimbly swings around and mounts her from the rear. Last summer I saw somewhat similar behavior in *X. nervosus* Banks: the male seemed to

recognize the female only by touch, when he came in contact with her he immediately placed several of his feet upon her, she drew her legs close to her side and he got upon her dorsum. Also in *Misumena aleatoria* I saw, on several occasions, that the minute male always found the female by touch, and quickly climbed upon her. In this family, accordingly, even though diurnal, there is no courtship and the male gains the female by superior agility aided by his smaller size.

The lycosids comprise crepuscular and nocturnal species, few of them hunting in the sunlight. Menge (1877) observed a female of *Trochosa terricola* Thor. build a nest in moss, and a male lying for hours before this hole "striking lightly here and there with the palps and fore legs," after which the female allowed him to embrace her. A similar courtship was seen by Mrs. Treat (1879) in another lycosid, the species not positively identified; the female lives in a silken burrow which the male approaches very cautiously; she "slowly advances to meet him, and he slowly retreats from the mouth of the den, moving backward while she moves forward, just reaching him with the tips of her fore legs as if caressing him"; this backward and forward progression of the two is repeated many times. Observations on other lycosids have been made by me (1903). In *Lycosa bilineata* (Em.) (*L. ocreata pulchra* Montg.) the anterior male tibiae are provided with thick brushes of vertical hairs, making them very conspicuous, but though the sexes recognize each other by sight there is no courtship; in one case a male simply jumped upon the female, in another after touching the female the male withdrew a little and quivered these legs slightly, the female moved towards him and he jumped upon her.

When the male stands before the female with these legs flexed, as he does, with the patellæ close to the sides of his cephalothorax and his body crouched near the ground, the tibiae are more horizontal than inclined upward. This, then, is not the best attitude to exhibit them to the female. . . . On this account this bristling of the tibiae can hardly

be regarded as a sexual ornament that is exhibited to charm the female. Further, it may be noted that this position of the first pair of legs is also assumed by the female when roughly handled or frightened; it is an attitude of defense of the species, not of sexual exhibition.

In *Lycosa ocreata* Hentz (*L. stonoi* Montg.) the tibiae of the first legs of the male are similarly provided with a brush of hairs, and he is darker than the female, but there is a pronounced courtship by the male consisting of rhythmically repeated waving of these legs with a jerking of the whole body backward and forward. Sight plays a considerable part in the approach of the sexes, but "apparently the first recognition of sex is by touch" for the courtship does not commence until the male has touched the female. In *L. lepida* (Keys.) the male is smaller and more brightly colored, and exhibits a simple courtship, shaking in the air his fore-legs that are only slightly elevated above the ground (his body may be prone). In *L. scutulata* Hentz there is "a decided courtship; the male differs from the female in his smaller size and in the black color of a portion of his fore-legs, and these legs (and the palpi also) are moved in a particular manner during the courtship. Observation shows that the male recognizes the female as such at a distance of at least six inches. The male's approach to the female is very slow, a kind of creeping, not at all similar to the vehement approach of certain other Lycosids. . . . The female, if eager, gives the signal of willingness to the male by touching him lightly with her first pair of legs, when he immediately embraces. In the observed cases, with one exception, the female killed the male at the end of the copulation." In *Pardosa nigropalpis* Emerton the males are smaller, and there "is a marked sexual color difference, the male being deep black and the female more brownish. . . . The advances are made by the male, and there is a distinct courtship process, which a vigorous male may maintain for two or three hours at a time with few interruptions when the female is recalcitrant. . . . The courtship motions are as follows:

The male stands with his body well elevated above the ground (an attitude that the female takes only when she is aggressive) on his three posterior pairs of legs, his head higher than his abdomen. . . . He waves his palpi upward in the air (*i. e.*, straightening them out before his head) and flexes them outward, from one to three times, then draws his body slightly backward and downward, rapidly waving in the air the outstretched palpi and first pair of legs, and spasmodically shaking the whole body with the violence of the movement. . . . The male recognizes a female as such immediately on touch; whether he recognizes her by sight alone I can not tell. In courting a fleeing female the male appears to follow her mainly by sight," but only when she is moving. In lycosids, accordingly, there is no courtship or else a complicated one; sex recognition is by touch alone, or by touch and sight combined.

For the attids we have a considerable number of observations. Seidel (1847) states that at the time of mating several females of *Salticus scenicus* Hahn seek out one male and live with him. But the greater part of our knowledge on this group is due to the Peckhams. In 1889 they described the courtship of *Saitis*, *Epiblemum*, *Icius*, *Hasarius*, *Synageles*, *Marptusa*, *Phidippus*, *Dendryphantes*, *Zygoballus*, *Habrocestrum*, *Philaeus* and *Astia*, with full delineations, accompanied by excellent drawings, of the posturings and movements of the male, which in some species are the most complex yet known. There are peculiar jumping and wheeling movements constituting dances, besides erection and display of those parts of the body that are strikingly colored and modified. We have not space here to repeat their descriptions and could not, indeed, do justice to them in a short summary; the reader should refer to the original memoir. In a following paper (1890) these authors describe the courtship of *Habrocestrum*, which is peculiar in that a male exhibits an ornamentation of the third pair of legs, and they give new figures of the attitudes of *Synageles picata*.

In their last study (1909) they figure the male posturings in *Pellenes* and *Euophrys*—in *E. monadnock* the male taking such a pose as to display at once the yellow palps, the heavily bristled, black first leg pairs (held elevated), and the orange femora of the third and fourth pairs.

Finally, I would add the observations made by me last summer on a considerable number of pairs of the large *Phidippus purpuratus* C. Koch. Here the male is not much smaller than his mate, but much darker and with more iridescence. A male will court on sight of a female, without first touching her; his motions consist of elevation of the cephalic region, raising and outspreading the first leg pair (with some waving of them), accompanied with advance towards the female and retreat from her as well, as side-stepping. After a male has once courted and won a mate, if he is kept in the same cage with her, he thereafter courts to much less degree, and finally not at all, before embracing her; that is, he would seem to have lost his fear of her, and indeed the pregnant female will more frequently run away from him than he from her.

IV. INTERPRETATION OF THE COURTSHIP PHENOMENA

Preliminaries to mating, whereby one individual seeks to gain the favor of another, constitute what we mean here as courtship. My previous definition (1903) of it, "a rhythmically repeated set of motions on the part of the male," was incomplete in limiting the process to one sex, for the female also may take part. Some mode of courtship would then occur where there is no immediate seizure of the female by the male, and where one of the individuals, generally the male, is the more eager.

In some cases there is no courtship, where the male is as large or larger than the female, the male seizing the female—sometimes appropriating her when immature, and mating with her shortly after her last moult. And in the thomisids the male captures his mate by superior agility. But more usually there is some form of courtship, and this may be by either touch or sight.

In the case of courtship by touch, the simplest form, in Drassids, *Dictyna* and some Agelenids, is that where the male after recognizing a female by touch taps her rapidly with his feet until she either runs from him or else becomes quiet and submissive to his embrace. The more complex form is found among the snare-makers, especially epeirids and theridiids, and the courtship is by signal pulls upon the lines of the snare; in this way the male not only locates the position of the female upon her snare, but he also ascertains whether she is eager for him, for when she is eager she returns his signals in the same way.

Courtship by sight is found most highly developed in the attids, less complicated in the more corpuscular lycosids, but not at all in the diurnal thomisids; it is not, accordingly, characteristic of all diurnal species. The courtship movements of the male range from a simple waving of the first leg pair, or waving of these and the palpi, to much more complicated movements of these parts associated with peculiar posturings, advances and retreats, and side-wheeling.

This brings us to the important question, just what psychical and physiological elements enter into the courtship? We can most clearly discuss this by considering the sexes in turn. Without question the chief psychical condition is sexual desire, in the case of the male, resulting from a physiological state due to internal secretions at the time of maturity. But with it is associated an inhibiting factor, the male's fear of the female. When the male is as strong as the female he exhibits no special fear of her, she is rather distinctly timorous towards him, then he does not court but seizes her by force. But in most species the male is smaller, in some cases very much smaller, than the female, and in all such instances he indicates great caution in approaching her, which is a demonstration of fear on his part. Adult females are decidedly more pugnacious than males, and contests between females are generally fatal to one of the contest-

ants, while this is seldom the result in battles between males. I once saw a male of *Phidippus purpuratus* kill his mature mate, and McCook (1890) has listed such cases in agelenids; but such happenings are very rare, and occur only when the male is as powerful as the female. In the great majority of species the male is decidedly afraid of the mature female, at least until after he has mated with her, and he does not exhibit towards her those aggressive movements which she often displays towards him. His embrace need not mollify her, for in certain epeirids and lycosids she has been seen to kill him immediately after the mating. It is interesting to note that one of the most general motions made by the male in courtship is the raising and extension of the forelegs towards the female, which is but a modification of a spider's general attitude of defense—a motion exhibited by both sexes when strongly disturbed.

Now there is courtship by the male only when he does exhibit this fear. Accordingly, we may conclude that courtship by the male spider results from a combination of the state of desire for and fear of the female. This explains satisfactorily why in some cases there is courtship while in other cases there is not. Courtship by the male continues until he has learned that the female is not hostile towards him; and his successive advance and retreat in her direction gives him the opportunity of experiencing, so learning, her degree of aggressiveness. By this courtship he advertises himself as a male, for no female shows such movements; and he may at the same time prominently display his ornamentation.

But we have neither reason to suppose that he is conscious of influencing the female thereby, nor that he is conscious of exhibiting particular personal attractions towards her. For in those lycosids where there is little secondary sexual difference the male may have as complex courtship movements as in cases where he is more ornamental. And it is assuming too much about a spider's mentation to postulate that the male is not only

conscious of his beauties, which are generally so placed that he can not perceive them himself, but has also an idea that he may arouse the female's esthetic sense. The Peckhams remark (1890, p. 122):

That whatever fine points of color or structure the male possesses, his actions before the female display them to the very best advantage; indeed, he *seems* to have a strong consciousness of every advantage, and to sedulously strive to bring it to the notice and impress its beauty upon the mind of the female to whom he is paying his addresses.

But they add a modifying foot-note:

We do not say that, in our opinion, he *is* conscious of his strong points. It is quite conceivable that the tendency to perform the antics may have developed along with the beauties which they serve to display without any idea of this existence dawning in the mind of the spider.

I think we should, until we have evidence to the contrary, accept as the correct interpretation the suggestion stated in that last sentence of the Peckhams, *i. e.*, that the male is not conscious that he is influencing the female, either sexually or esthetically.

We have just seen that the raising of the forelegs in courtship is but a modification of the general attitude of defense, therefore not primarily for display. The waving of the palpi may follow any excitement, is also not exclusively sexual. And I have been interested in finding a partial explanation of a male attitude exhibited by certain attids, namely the lateral flexion of the abdomen. In *Phidippus purpuratus* the male at frequent intervals in his courtship touches his spinnerets to the ground, thus attaching a silken line, and then in his side-wheeling before the female, with closed spinnerets, this line pulls his abdomen to one side. Such flexion of the abdomen, at least in this particular species, is thus not a conscious effort of display, but is due to a simple tension of the ordinary drag-line.

Last summer I observed in several species the curious phenomenon of males courting one another in the same way as they do females. I placed in a small cage two males of *Pardosa pallida*, Emert., and they moved their

fore-legs and palpi just as in normal courtship. Two males, a smaller and a larger, of *Phidippus purpuratus* were placed together; the larger was aggressive, the smaller exhibited towards him normal courtship motions. In neither of these cases were females present. Two males of the brilliant *Phidippus mccoockii* Peck. on being placed in one cage, on several different occasions, raised the legs, side-wheeled, and flexed the abdomen laterally, resembling a courtship; I had no female of this species to determine the normal courtship, but to females of *P. clarus* Koch they acted in the same way. Two males of *Zygoballus bettini* Peck. were placed in a cage and watched each other attentively, but without courtship; an immature female was introduced, when each male proceeded to court her: advancing and retreating by short quick steps, the first legs raised vertically and parallel and these and the palpi twitching; the female ran away from both, and after I had removed her the males exhibited the same movements towards each other, with the only difference that the raised legs were somewhat divergent and that the smaller male fled when the larger came too near. Evidently in these cases the males mistook one another for females, which would indicate that their visual discrimination is far from precise—perhaps less than that of the females.

The female is also actuated by sexual desire, sometimes quite as strongly as the male; this is the case with *Theridium tepidariorum*, where the female seems insatiable, and the Peckhams (1889) observed a female of *Saitis pulex* approaching a male with courting movements. In theridiids and epeirids the female signals along the snare lines quite as vigorously as the male does.

But whenever she is larger than the male, she exhibits as a rule, no great fear of him. She may express her desire to the male by remaining quiet and passive, or by touching him gently or moving towards him, or by counter-signalling by means of lines of her snare; and sometimes she may take the initiative in this. Where

the courtship is by touch it is wholly excluded that the female can have any esthetic appreciation of the male, she is actuated either by sexual desire or by its absence. But where there is courtship by sight, as in the attids and some lycosids, the Peckhams have consistently maintained that the female is influenced by an esthetic appreciation of the colors, ornaments and postures of the male, and that she chooses that male that pleases her esthetic sense; and they have reiterated this view in their last paper (1909) without referring to my quite different interpretation (1903). Now there is no doubt that, as the Peckhams have shown, when there is courtship by sight the female attentively watches the male, and also no doubt that the male's motions are generally such as to exhibit his colors and ornaments to the best advantage; an exception to this is that the male of *Lycosa bilineata* exhibits no courtship although his fore-legs are provided with thick brushes of hairs. Then there is the interesting observation (Peckham, 1889) that of the two male forms of *Astia vittata* the female always selects the more ornamented *niger*-variety, which is darker and possesses plumose tufts on the cephalothorax, though it is not stated in how many cases this was observed. But it is significant that the *niger*-form "is much the more lively form of the two"; it might then be the case that the female selects him not because he is more ornamented, but because he is more lively,—therefore because he more quickly advertises himself as a male. This seems to me to be the correct understanding of the matter. For just as we have no evidence that the male consciously endeavors to exhibit his attractions, we have also no evidence that the female is influenced esthetically. What we do know is that the male by his courtship, a set of motions resulting from the conflicting states of sexual desire and fear, exhibits or advertises himself as a male; and that the female on sight of this courtship recognizes him as a male and accepts him if she be eager, or else becomes gradually stimulated by watching him. In other words, too great an assumption is made in supposing the female to have an esthetic sense, while it is

more probable that the female is attracted by maleness alone and not by beauty. The immediate effect of courtship on the female is the stimulation of her sexual desire by recognition of a male; not first the arousing of an esthetic sense and second the arousing of sexual feelings. On my interpretation the case in *Astia* may be explained simply and without assumption: the *niger*-form is selected by the female because he is more different in color and structure from her than is the other male form, consequently is more quickly recognized as a male; this is what determines her, and not color or ornaments. The significance of peculiarities in color, structure and movements of the male lies in insuring quick sex-recognition, not in arousing esthetic feelings. The case of *Astia* is the only one known in which the female seems to exert a choice between males, dimorphism of males being rare in spiders.

We conclude, accordingly, that the male in visual courtship is not actuated by a conscious effort to exhibit his peculiar beauties, and that the female does not select males by an esthetic sense. Courtship by the male results simply because fear is mingled with his desire; and probably the female will accept the first male who courts her, and makes himself recognized as a male, at the time when she is physiologically desirous. Sexual selection in the meaning of Darwin, accordingly, and in opposition to the views of the Peckhams, has probably played no part in the evolution of the secondary sexual differences of spiders.

V. THE NATURE AND USE OF THE SECONDARY SEXUAL DIFFERENCES

We are not concerned here with the question of the first origin of secondary sexual differences, *i. e.*, whether they have arisen as gradual fluctuations, as Darwin held for the most part, or from acquired traits becoming inherited on the view of Cunningham (1900), or from sudden mutations as Morgan (1903) has suggested, for there is no observational evidence from which we can reason. We

have rather to consider their value to the species, what is their use, and the factors which have served to perpetuate them.

In the first place it will be convenient to name categorically the main classes of secondary sexual characters found in animals in general, and second to discuss the significance of those found in araneads.

Plate (1908) has furnished a useful tabulation of secondary sexual characters, devised mainly to show "what an enormous morphological field is comprised in this term." The following arrangement of such characters is simpler than his, though as comprehensive, and will be more convenient for our present discussion.

1. Weapons employed by males in their combats with one another.

2. Characters used for sexual recognition and sexual stimulation.

3. Characters of more immediate value in ensuring approximation of the sexes and copulation.

4. Characters of value in provision for and nurture of the progeny.

5. Characters due to habitudinal differences of the sexes.

6. Characters of value in protecting a particular sex against other species.

We may next determine how these six main groups of characters are represented in spiders.

1. The weapons employed by males in their fighting for the possession of females are readily explained, as Darwin did in the first part of his theory of sexual selection, as being perpetuated by a natural selection between males.

Such direct combats between males do not appear to occur among spiders, neither do the males possess peculiar weapons, unless peculiarly modified chelicera may be considered as weapons. Mature males when placed together will frequently fight, but the Peckhams (1889) in describing this in the case of an *Icius* conclude that the battles are probably sham affairs, rarely resulting disastrously, and "gotten up for the purpose of displaying

before the females." There may be more fighting between males when females are present, though there is no good evidence on this matter; but we have no reason to suppose that the males consciously endeavor to exhibit their prowess any more than they consciously try to display their ornaments. Males of the attid *Icius palmarum* placed in small cages were not observed by me to fight, nor were males of *Phidippus mccoookii* nor those of *Zygodallus bettini*; but fighting of males was noticed in *Ceratinopsis interpres*, *Geotrecha pinnata* and *Xysticus nervosus*, and in the last species a male would leave the back of a female to fight a rival. But, as the Peckhams found, no injuries result to the males from this fighting, therefore these are not serious combats, and only once have I seen a male kill another male of his species (in *Prosthesima atra*).

Male spiders also do not possess intimidation organs, which result when weapons become hypertrophied according to the views of Guenther (1909):

2. Characters for sexual recognition and stimulation may be subdivided according to the sense organs which they affect, as Jäger (1874) has indicated. As we have seen, the only senses concerned in the case of spiders seem to be those of touch and sight. It may be that certain of the tactile organs, probably certain of the jointed spines, may become more numerous or more specialized at maturity to aid in sexual recognition, but this point remains to be tested. But those secondary sexual characters of male spiders found only where there is courtship by sight, such as ornamental colors and structures, and posturings that display them, fall under this category. Such are the male differences, as the Peckhams have shown, in the chelicera, clypeus, palpi and legs, that is, "in those parts of the animal that are plainly in view when the male is paying court to the female." Thus the chelicera may be lengthened, curved or spinous; the clypeus may be heightened or bear prominences; the first pair of legs may be thickened or have tufts of hairs; and any or all of these parts may have conspicuous color

markings. These differences are so pronounced in the attids that in many cases the species is known only by one of the sexes. We have previously seen that conscious esthetic choice by the female probably does not account for such male characters, that they are, accordingly, probably not due to sexual selection. These characters of the males may be most readily explained as being conserved by simple natural selection. Peculiar male ornamentation would be selected because it insures quicker sex-recognition, therefore prompter mating. The male is thereby more surely accepted by the female, not selected by her in the sense of Darwin. The process is much more an announcement of sex by the male than a choice by the female, and results in the female accepting the sex rather than the individual. There is no reason to suppose the female spider is actuated esthetically, while we do know she is actuated sexually—in some cases quite as much as the male is. There is no need of calling in any other factor than natural selection.

Whether such ornamental male characters, which stimulate the visual sense of the female, subserve sex recognition rather than sex stimulation we are hardly able to decide in the absence of any thorough analysis of the psychical states of spiders. But probably a female would first have to recognize a male as a male before she became sexually aroused by him, and for this reason male ornamentation would seem to be primarily to insure sex-recognition rather than sex-stimulation.

In opposition to the views of Wallace (1889) the Peckhams (1890) have correctly argued that the ornamentation of male spiders is not due to any "higher degree of vitality" of the males, for the female seems to be in all respects fully as active as the male, and at maturity even more active. The same objection may be made against the concept of Geddes and Thomson (1897) with regard to differences of the sexes.

The Peckhams have found in the attids, in agreement with Darwin's conclusions for birds, that: (a) when the adult male is more conspicuous than the adult female, the

young of both sexes more closely resemble the adult female; (*b*) when the adult female is more conspicuous than the adult male, the young of both sexes more closely resemble the adult male; and (*c*) when both adults are alike the young of both sexes resemble them.

3. Characters of value after the act of sex-recognition to insure efficient mating would seem to be various, and all probably perpetuated by natural selection. Such would be the relatively larger legs in the case of certain males, in so far as they serve to hold the female. Smaller size and greater agility of the male, not a frequent phenomenon in araneads, would also aid in the mating by enabling the male to move more quickly upon the snare of the female, and to escape more rapidly from her should she be aggressive.

4. Characters of value in providing for and nurturing the young are limited in spiders to the female, and are also perpetuated by natural selection. Such are the greater size of the abdomen to accommodate the eggs, and the gland whose function is to agglutinate them. Such is also the greater pugnacity and bravery of the female, which is probably the expression of her greater need of food.

5. Characters due to habitudinal sex differences are few in spiders. Such differences first become marked at maturity, as do the other secondary sexual characters, all being in some way connected with internal secretions formed during the elaboration of the genital products. In the epeirids, as shown by me (1908*b*), immature males have the same mode of life as their sisters, and "construct perfect snares of the types of those of their respective females. But the adult males . . . do not spin snares at all, but build nests near those of adult females." Indeed, it is quite general among snare-making species that adult eager males regularly leave their snares to live upon or near those of females; and adult males of lycosids and drassids, which make no snares, leave their nests to seek for females. The chief habitudinal difference, accordingly, is that while the female continues a more or less

sedentary existence, or makes excursions mainly for food, the male in many species becomes a wanderer when he is adult, searching for a mate. The male thus comes to spin less and to run more; and a morphological consequence of this habit is seen in the total or nearly complete loss of the cribellum, or spinning plate, by adult males of certain species. It is possible his relatively greater leg length may be in some cases also associated with this habit. These few cases would fall in line with the theory of Cunningham (1900), being characters due to difference in mode of life of the sexes. But all such phenomena would be likewise regulated by natural selection.

6. The secondary sexual characters which operate to protect a particular sex in the struggle for existence are found mostly in the females, and these would be subservient to natural selection. In certain spiders, as notably some epeirids (*Argiope*, *Acrosoma*, *Gasteracantha*), the female is not only much larger than the male, but also much more brightly colored, often with most conspicuous black and yellow or red and yellow markings; and in *Acrosoma* and *Gasteracantha* the abdomen may be drawn out into angular processes and spines. We can not accept for this case the Peckhams' suggestion that this is due to difference of mode of life of the sexes, for so far as is known the males of these have the same mode of life as those of other epeirids. These brilliant and remarkable females all build their snares in the open sunshine, and remain upon the centers of the snares. They would seem rather to represent cases of warning coloration, this ultimately protective to the possessors: in *Acrosoma* and *Gasteracantha* the bright markings would serve to advertise the hard and spinous abdomina, and in *Argiope*, which is soft-bellied, perhaps to announce the large snare. Possibly the brushes of hairs on the legs of another female epeirid, *Nephila*, would be an example of warning characters calling attention to the unusually large and powerful web, thus protecting the snare against birds. It is always difficult to be sure of a correct interpretation of phenomena of this kind, but it would seem probable

that some cases of brighter female coloration represent examples of warning coloration, and consequently come under our sixth category of secondary sexual phenomena.

It will be recalled that Wallace (1889) explained the general less conspicuous coloration of female birds on the ground of their need of greater protection, since they play the major rôle in guarding the nest and the eggs. The Peckhams (1889) have argued that this idea would not apply to the general inconspicuous coloration of female attids, because when they have eggs they hide these and themselves within thick silken nests and so are sufficiently protected from enemies. But I believe Wallace's explanation will apply in the case of spiders. For the males do not develop their ornamentation until maturity, and they have much less need of protection than the females because they live usually not much longer than a few weeks after maturing, and take no part in the care of the young. The males have fulfilled their main function after impregnating the females, and they are of no use to the species thereafter. But the females live at least several months after maturing, in some cases several years, and they have the whole care of the eggs and young. In araneads, as in all animals, the females are of the greater importance in the perpetuation of the race. Therefore it is probable, in agreement with Wallace, that natural selection has generally maintained a more protective coloration of the female.

In all six categories of secondary sexual characters in so far as spiders are concerned, accordingly, natural selection alone is sufficient to explain the regulation of the phenomena. At the same time these phenomena would seem to have a manifold origin, as they certainly fulfill very different uses.

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